Reproductive biology of the smoothhound, *Mustelus mustelus* (Chondrichthyes: Triakidae) from the coast of Senegal (eastern tropical Atlantic)

by

Christian CAPAPÉ (1), Youssouph DIATTA (2), Mansor DIOP (2),
Yvan VERGNE (1) & Olivier GUÉLORGET (1)

ABSTRACT. - The smoothhound shark, *Mustelus mustelus* (Linnaeus, 1758), is commonly landed at fishing sites along the Senegalese coast (eastern tropical Atlantic). Adult males and females are captured mainly in spring and summer. The smallest male adult was 82 cm TL and weighed 1.85 kg. Males were all adults by 95 cm TL. The smallest female adult was 90 cm TL and weighed 3 kg. Females were all adults by 104 cm. The largest male and the largest female were 139 cm and 150 cm TL, and weighed 11 kg and 8.1 kg. However, the heaviest female weighed 13.85 kg and was 145 cm TL. There was no significant relationship between total mass and TL between males and females. Mating probably occurred in spring and early summer, as did parturition. Gestation lasted approximately one year. Females had an annual reproductive cycle, although some females reproduce in alternate years. Diameters of the largest yolky oocytes ranged from 20 to 23 mm (mean 20.7 ± 3.4) and their masses from 3.6 to 4.9 g (mean: 4.2 ± 0.3). Both uteri were compartmentalized into chambers during part of the pregnancy, with a single embryo in each chamber. Size and mass at birth, based on term embryos and neonates ranged from 36 to 45 cm TL (mean: 40.31 ± 1.72) and from 150 to 256 g (mean: 199.9 ± 20.7). In order to show the role of mother during embryonic development, a chemical balance of development was calculated, it was based on mean dry masses of the largest yolky oocytes and term embryos was 24. Ovarian fecundity is slightly higher than uterine fecundity. Litter sizes ranged from four to 21 (mean: 9.2 ± 3.9), and there was a slight positive relation between litter size and total length of females. In free-swimming specimens, only sub-adult females significantly outnumbered the male ones.

RÉSUMÉ. - Biologie de la reproduction de l'émissole lisse, *Mustelus mustelus* (Chondrichthyes: Carcharhinidae) de la côte du Sénégal (Atlantique oriental tropical).

L'émissole lisse, *Mustelus mustelus* (Linnaeus, 1758) est une espèce de requin abondamment débarquée sur les sites de pêche situés au long de la côte sénégalaise (Atlantique oriental tropical). Des mâles et femelles adultes sont généralement capturés au printemps et en été. Le plus petit mâle adulte mesurait 82 cm de longueur totale (LT) et pesait 1,85 kg. Au-dessus de 95 cm LT, tous les mâles observés étaient adultes. La plus petite femelle adulte mesurait 90 cm de longueur totale (LT) et pesait 3 kg. Au-dessus de 104 cm LT, toutes les femelles observées étaient adultes. Les plus grands adultes mâle et femelle mesuraient respectivement 139 cm et 150 cm LT et pesaient respectivement 11 kg et 8,1 kg. Toutefois, la plus lourde femelle pesait 13,85 kg et mesurait 145 cm LT. Il n'y a pas de relation significative taille-masse entre mâles et femelles. L'accouplement et la parturition ont lieu au printemps et au début de l'été. La gestation dure approximativement une année. Les femelles ont un cycle de reproduction annuel, bien que certaines femelles se reproduisent une année sur deux. Les diamètres des plus grands ovocytes riches en vitellus sont compris entre 20 et 23 mm (moyenne : 20,7 ± 3,4) et leurs masses entre 3,6 et 4,9 g (moyenne : 4,2 ± 0,3). Les deux utérus sont compartimentés en chambre et dans chacune d'elles un unique embryon se développe. La taille et la masse à la naissance, fondées sur les embryons à terme se situent entre 36 et 45 cm (moyenne : 40,31 ± 1,72) et de 150 à 256 g. Dans le but de mettre en évidence le rôle de la mère pendant le développement embryonnaire, une balance chimique de développement a été calculée ; elle est fondée sur les masses sèches moyennes des plus grands ovocytes et des embryons à terme et égale à 24. La fécondité ovarienne est sensiblement supérieure à la fécondité utérine. Les portées varient de quatre à vingt et un (moyenne : 9,2 ± 3,9) ; parmi les individus libres, il y a une faible corrélation positive entre le nombre d'individus par portées et la longueur totale des femelles. Parmi les individus libres, seul les femelles subadultes sont significativement plus nombreuses que les mâles.

Key words. - Chondrichthyes - Triakidae - *Mustelus mustelus* - ASE - Senegal - Reproductive biology.

Off the coast of Senegal, shark species are the focus of an intensive fishery, both commercial and artisanal, for human consumption. The flesh is dried and, under the vernacular name of "sali", is used locally or exported to other African countries. Fins of larger specimens are collected and prepared as "laâf", exported to Asian markets (Gueye-Ndiaye, 1993).

Landings of shark species in fishing sites located along the Senegalese shore offered us the opportunity to collect data and to describe some aspects of reproductive biology of those most frequently caught in the area, such as the dusky shark, *Carcharhinus limbatus* (Capapé *et al.*, 2004), the Atlantic weasel shark, *Paragaleus pectoralis* (Capapé *et al.*,

---

(1) Laboratoire d'ichtyologie, Case 104, Université Montpellier II, Sciences et techniques du Languedoc, 34095 Montpellier CEDEX 5, FRANCE. [capape@univ-montp2.fr]

(2) Département de biologie animale, Faculté des sciences et techniques, Université Cheikh Anta Diop, BP 5005, Dakar, SÉNÉGAL.

2005) and the milk shark, *Rhizoprionodon acutus* (Capapé, unpublish. data). In this paper, we complete our studies of local shark species, detailing size at sexual maturity, size at birth, relationship between mass and size, fecundity and sex-ratio of the smoothhound, *Mustelus mustelus*. Comparisons are made with previous information obtained from this species from other areas, especially off Tunisia (Capapé, 1974) and South Africa (Smale and Compagno, 1997).

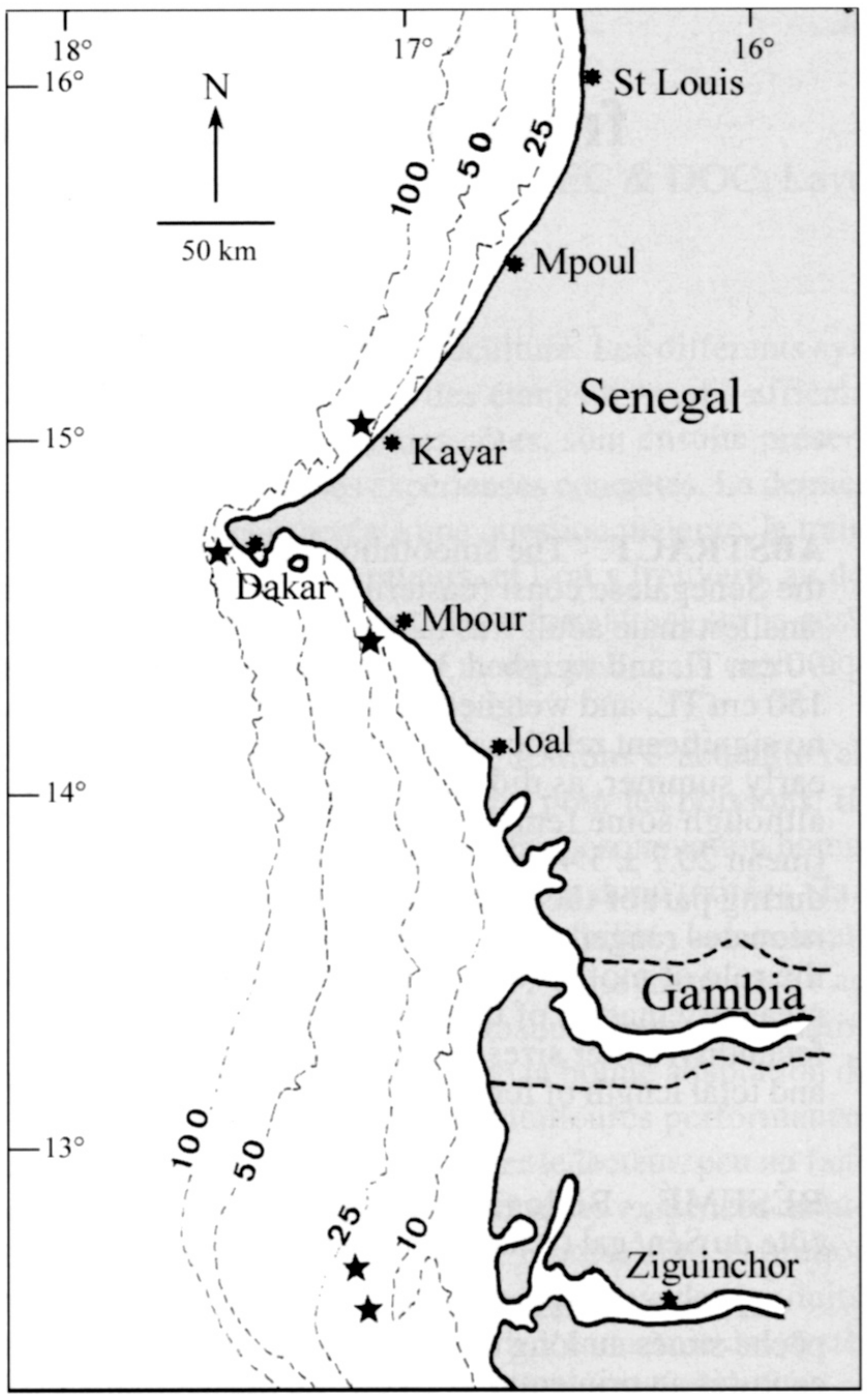

Figure 1. - Map of Senegal showing the landing sites and captures sites (black stars) of *Mustelus mustelus* (redrawn from Kébé and Le Reste, 1993). Depth contours in metres. *[Carte du Sénégal montrant les sites de débarquement et les sites de captures (étoiles noires) de* Mustelus mustelus *(redessiné d'après Kébé et Le Reste, 1993). Contour des profondeurs en mètres.]*

MATERIAL AND METHODS

A total of 272 specimens, 97 males and 175 females were examined; the monthly collection is presented in table I. In addition, 78 developing embryos and 221 term embryos were examined.

The specimens were caught by demersal gill-nets off the Senegalese coast from 1993 to 2004, at depths between 20 and 100 m, generally on sandy bottoms, occasionally on muddy or detritic bottoms (Fig. 1). In the same areas, *Mustelus mustelus* is caught together with the milk shark, *Rhizoprionodon acutus*, the Atlantic weasel shark, *Paragaleus pectoralis* and, a bit less, the dusky shark, *Carcharhinus limbatus*, (Fig. 1). Total length (TL) was measured to the nearest millimetre following Bass *et al.* (1975) and weight to the nearest gram. Clasper length (CL, mm) was measured according to Collenot (1969), from the forward rim of the pelvic girdle to the tip of the clasper. Developing and yolky oocytes and embryos were removed from the ovaries and uteri, respectively, sorted and then measured to the nearest mm and weighed to the nearest dg.

The onset of sexual maturity was determined in males from the condition and the length of claspers following Bass *et al.* (1975), Stevens and McLoughlin (1991) and Watson and Smale (1998).

The claspers of juveniles are shorter than pelvic fin length, flexible and not calcified, those of sub-adults are larger than pelvic fin length, flexible but slightly calcified. In adults, claspers are elongated, longer than pelvic fins length, rigid and calcified. Some aspects of the testes and other reproductive organs are described following Capapé *et al.* (1990, 2002) and Bridge *et al.* (1998). Size at sexual maturity was determined in females from the condition of ovaries and the morphology and the degree of development of the reproductive tract (Capapé *et al.*, 1990). In both males and females, specimens were divided in three categories: juveniles, sub-adults and adults.

Table I. - Monthly collection of *Mustelus mustelus* observed in the sample. *[Récolte mensuelle de* Mustelus mustelus *observée dans l'échantillon.]*

Category	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total
Males													
Juveniles	-	1	3	-	-	-	-	-	-	1	-	1	6
Sub-adults	-	4	3	1	-	2	-	-	-	-	2	-	12
Adult	6	3	1	14	14	12	7	6	4	3	4	5	79
Total	6	8	7	15	14	14	7	6	4	4	6	6	97
Females													
Juveniles	3	-	1	1	2	1	-	-	-	1	3	3	15
Sub-adults	6	3	2	1	9	10	1	-	3	2	4	3	44
Adults	4	7	5	21	31	23	16	5	2	-	-	2	116
Total	13	10	8	23	42	34	17	5	5	3	7	8	175
Grand total	19	18	15	38	56	48	24	11	9	7	13	14	272

To investigate the embryonic development and the role of the mother during gestation, a chemical balance of development (CBD) was considered. CBD is the mean dry mass of fully developed embryos divided by the mean dry mass of yolky oocytes or eggs. Water content of 50% in ripe oocytes and 75% in fully developed embryos was assumed, based on chemical analyses of the small spotted catshark, *Scyliorhinus canicula*, by Mellinger and Wrisez (1989). CBD is a tentative estimate.

Tests for significance ($p < 0.05$) were performed by using ANOVA, Student *t*-test and the chi-square test. The linear regression was expressed in decimal logarithmic coordinates. Correlations were assessed by least-squares regression. In the relationship mass *versus* total length, comparisons of curves were carried out by ANCOVA.

RESULTS

Size at sexual maturity

Males

During the juvenile stage, the claspers were short and flexible, both testes and genital ducts were slightly developed and membranous. Six juveniles were examined ranging in size between 39 and 66 cm TL and weighing between 195 and 660 g, including three neonates presenting an unhealed scar on their ventral surface, caught in March (Tab. I).

Twelve sub-adults were recorded, the smallest specimen was 70 cm TL and weighed 970 g, the largest 87 cm TL and weighed 2.2 kg. In sub-adults, the testes were developed, but no spermatocysts were externally visible and no sperm occurred in the seminal vesicles. The genital ducts were conspicuously visible and the *ductus deferens* (sensu Hamlett *et al.*, 1999; Callard *et al.*, 2005) was slightly convoluted. During this stage, their length rapidly increased concomitant with maturity (Fig. 2). Sub-adults were generally caught from February to April (Tab. I).

Seventy-nine adults were collected. The smallest specimen was 82 cm TL and weighed 1.85 kg, the largest 139 cm and weighed 11 kg. Males were all adult by 89 cm TL. The claspers were rigid, calcified and elongated. Spermatocysts were externally visible and the seminal vesicles contained sperm throughout the year. The ductus deferens was obviously convoluted. Adults were mostly landed from April to August (Tab. I).

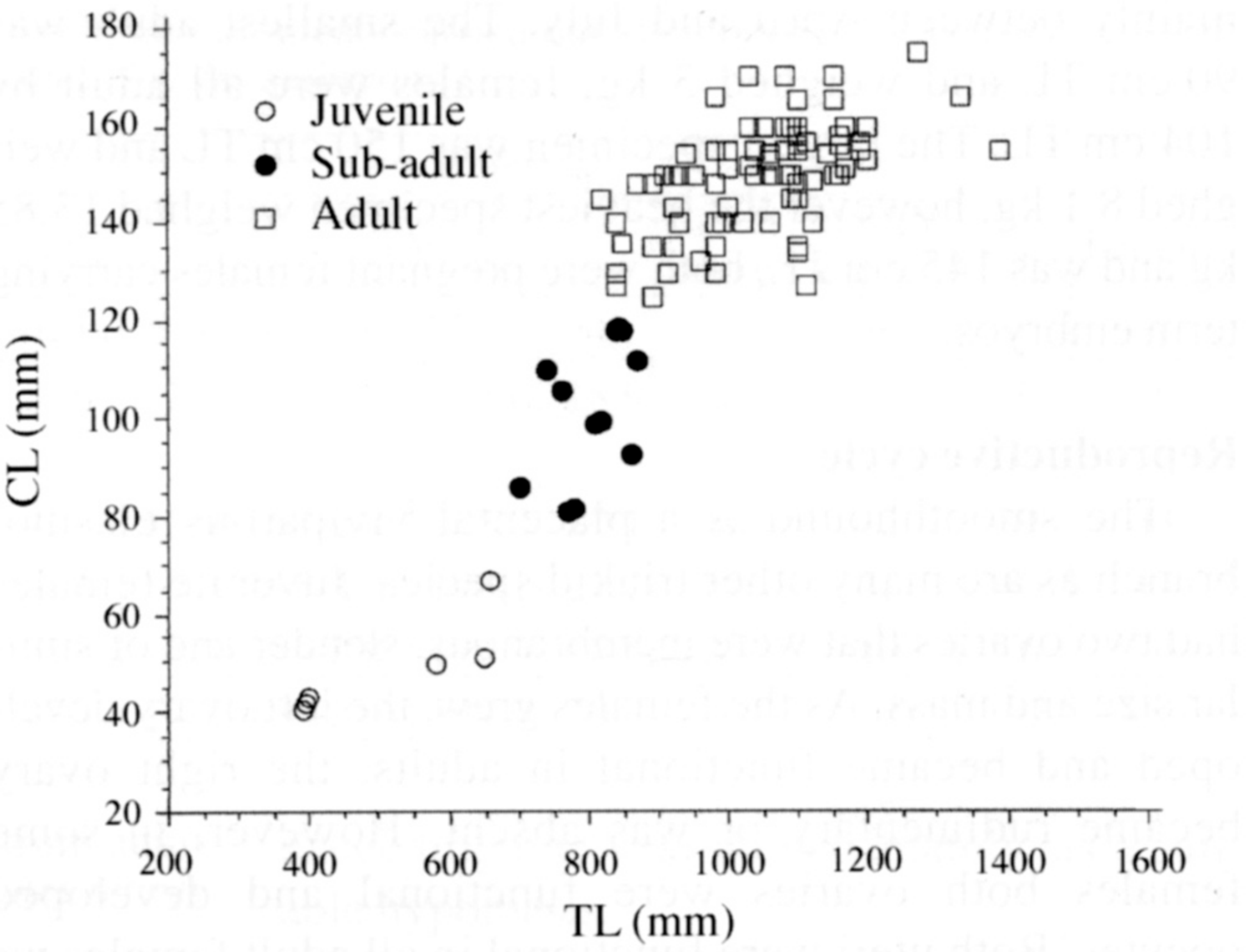

Figure 2. - Clasper length (CL) vs total length (TL) in male *Mustelus mustelus*. *[Relation entre la longueur des claspers (CL) et la longueur totale (TL) chez les mâles de* Mustelus mustelus.*]*

Females

During the juvenile stage the females, ranging between 39 and 84 cm TL and weighing between 201 g and 16.4 kg, had membranous ovaries, membrane-like oviducts, and inconspicuous oviducal glands. Of the 15 juveniles collected, two were neonates measuring 390 and 420 mm TL, the latter weighed 235 g. Juveniles were rather caught in January, November and December (Tab. I).

Forty-four sub-adult females were collected, mostly from May to June (Tab. I). The smallest specimen was 80 cm TL and weighed 1.63 kg, the largest specimen was 104 cm TL and weighed 4.15 kg. Sub-adult females presented ovaries with translucent oocytes, well-differentiated genital ducts and slightly rounded oviductal glands.

One hundred and sixteen adult females were collected

Category of adult females	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Total
Pregnant													
Carrying encapsulated eggs	-	2	2	8	8	10	9	-	-	-	-	-	39
Carrying developing embryos	-	3	2	4	2	-	-	3	1	-	-	2	17
Carrying term embryos	-	-	1	-	12	7	4	-	-	-	-	-	24
Total	-	5	5	12	22	17	13	3	1	-	-	2	80
Non-pregnant													
Post-partum	-	-	-	4	4	3	-	1	-	-	-	-	12
With vitellogenic activity	2	1	-	3	2	1	2	1	-	-	-	-	12
Inactive	2	1	-	2	3	2	1	-	1	-	-	-	12
Total	4	2	-	9	9	6	3	2	1	-	-	-	36
Grand total	4	7	5	21	31	23	16	5	2	-	-	2	116

Table II. - Monthly collection of adult females *Mustelus mustelus* observed in the sample. *[Récolte mensuelle de femelles adultes de* Mustelus mustelus *observées dans l'échantillon.]*

mainly between April and July. The smallest adult was 90 cm TL and weighed 3 kg, females were all adult by 104 cm TL. The largest specimen was 150 cm TL and weighed 8.1 kg, however the heaviest specimen weighed 13.85 kg and was 145 cm TL, both were pregnant females carrying term embryos.

Reproductive cycle

The smoothhound is a placental viviparous elasmobranch as are many other triakid species. Juvenile females had two ovaries that were membranous, slender and of similar size and mass. As the females grew, the left ovary developed and became functional in adults, the right ovary became rudimentary or was absent. However, in some females both ovaries were functional and developed oocytes. Both uteri were functional in all adult females we have examined.

Two categories of mature females were distinguished, pregnant and non-pregnant (Tab. II). Of the 80 pregnant females sampled, 39 carried encapsulated eggs, 17 had developing embryos and 24 had term embryos. The 41 females carrying embryos showed vitellogenic activity. Their ovary produced cohorts of oocytes similar in diameter and in mass. As embryos grew in both uteri, a cohort of oocytes enlarged and produced yolk in the ovary. So, soon after parturition, the females will mate and conceive again. Forty-two yolky oocytes were measured; their diameter ranged between 20 and 23 mm (mean: 20.7 ± 3.4) and their mass between 3.6 and 4.9 g (mean: 4.2 ± 0.3). All the oocytes found in pregnant females with developing embryos were less than 16 mm diameter. A single near-term female was caught in March (Tab. II; Tab. III, record 9), 12 other specimens were caught in May, seven in June and four in July (Tab. II, IV).

Females carrying encapsulated eggs were caught from February to July, mainly between April and July. Fertilized eggs were enveloped in a diaphanous and brownish capsule ending with a large twisted filament at both ends. Twenty-two encapsulated eggs were removed from females at the beginning of gestation. Capsules and fertilized eggs were measured and weighed separately (Tab. V). Fertilized eggs were slightly heavier than yolky oocytes, due to the fact that

Table III. - Reproductive cycle of female *Mustelus mustelus*. Condition of ovary and uteri during gestation. *[Cycle de reproduction des femelles de* Mustelus mustelus. *Etat de l'ovaire et des utérus pendant la gestation.]*

Record number	Month of catch	Size of female (TL, cm)	Mass of female (kg)	Ovarian activity	Oocyte diameter (mm)	Oocyte number	Uterine content	Embryo size (TL, mm)	Embryo mass (g)	Embryo or egg number (left + right)	Male (M) + female (F) embryos
1	Feb.	113	5.50	-	-	-	Eggs	-	-	3+4	-
2	Feb.	112	4.90	Vitellogenesis	15-16	6	Embryos	200-201	40-45	2+2	2M +2F
3	Feb.	115	5.70	Vitellogenesis	13-15	8	Embryos	210-225	41-46	2+2	1M + 2F
4	Feb.	126	9.70	Vitellogenesis	15-16	10	Embryos	190-210	41-45	4+6	4M + 6F
5	Mar.	92	3.00	-	-	-	Eggs	-		3+1	-
6	Mar.	127	8.90	-	-	-	Eggs	-	-	6+8	-
7	Mar.	109	5.30	Vitellogenesis	14-16	6	Embryos	279-292	60-65	2+2	2M + 2F
8	Mar.	127	8.90	Vitellogenesis	13-15	14	Embryos	300-340	73-89	7+6	6M + 7F
9	Mar.	131	10.00	Vitellogenesis	21-22	16	Term embryos	375-410	160-230	7+7	7M + 7F
10	Apr.	130	8.70	Vitellogenesis	14-15	14	Embryos	302-310	66-74	6+7	6M + 7F
11	Apr.	131	10.00	Vitellogenesis	14-15	14	Embryos	345-355	106-130	5+4	3M + 6F
12	Apr.	135	10.80	Vitellogenesis	13-14	12	Embryos	330-350	99-112	4+8	7M + 5F
13	Apr.	142	11.50	Vitellogenesis	14-16	16	Embryos	310-350	96-110	4+7	7M + 4F
14	May	147	7.25	-	-	-	Eggs	-	-	12+12	-
15	May	126	8.20	Vitellogenesis	15-16	14	Embryos	350-375	114-122	4+4	2M + 6F
16	May	127	8.79	Vitellogenesis	15-16	16	Embryos	305-330	90-100	7+7	6M + 8F
17	May	134	9.10	Vitellogenesis	21-22	16	Term embryos	380-440	163-245	6+6	5M + 6F
18	Jun.	139	9.85	Vitellogenesis	21-23	18	Term embryos	376-440	164-235	7+7	7M + 7F
19	Jul.	138	9.70	-	-	-	-	-	-	6+8	-
20	Jul.	135	9.10	Vitellogenesis	21-22	14	Term embryos	366-400	155-196	6+6	3M + 9F
21	Aug.	124	9.00	Vitellogenesis	12	10	Embryos	100-115	8.4-10.8	5+5	5M + 5F
22	Aug.	135	8.90	Vitellogenesis	11-déc	12	Embryos	112-123	9.2-10.6	5+5	4M + 6F
23	Aug.	139	10.00	Vitellogenesis	11-déc	10	Embryos	108-122	9.2-12.1	5+5	5M + 5F
24	Sep.	145	13.85	Vitellogenesis	déc-13	12	Embryos	115-126	9.1-13.6	6+6	6M + 6F
25	Dec.	114	5.25	Vitellogenesis	13-14	10	Embryos	175-192	23-29	3+3	3M + 3F
26	Dec.	126	10.00	Vitellogenesis	14	12	Embryos	170-185	25-29	6+6	6M + 6F

Table IV. - Near-term female *Mustelus mustelus* observed in the sample with measurements carried out in embryos. *[Femelles à terme de* Mustelus mustelus *observées dans l'échantillon avec mensurations réalisées chez les embryons.]*

		Females						Embryos									
		TL (cm)			TM (kg)			TL (mm)			TM (g)			In left uterus	In right uterus	Male	Female
Month	n	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	n	n	n	n
Mar.	1	131	-	-	10.0	-	-	375-425	396	12.6	160-230	193.6	18.9	7	7	7	7
Apr.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
May	12	104-134	117.7	9.0	4.50-9.10	6.154	1.358	380-440	406	15.9	164-245	205.8	20.1	40	42	39	43
Jun.	7	113-139	129.1	10.3	5.00-10.00	7.961	2.101	360-450	404	19.3	165-256	198.1	21.2	42	41	40	43
Jul.	4	124-135	129.2	5.1	8.00-10.00	9.025	0.818	366-425	395	13.9	155-230	193.9	18.8	22	20	16	26
Total	24	104-139	123.5	10.2	4.50-10.00	7.320	1.942	360-450	403	17.2	155-256	199.9	20.7	111	110	102	119

Table V. - Measurements carried out on encapsulated eggs removed from adult female *Mustelus mustelus*. *[Mensurations réalisées sur des œufs encapsulés retirés chez des femelles adultes de* Mustelus mustelus.*]*

Measurements		Total length (mm)			Width (mm)			Mass (g)		
	n	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD
Capsule	22	335-375	356.1	12.5	-	-	-	3.7-4.9	4.2	0.4
Fertilized egg	22	3.1-4.3	3.6	0.4	2.0-2.4	2.1	0.1	3.6-5.8	4.9	0.7

they were surrounded by a clear jelly-like fluid probably extruded by oviductal glands (Hamlett *et al.*, 2005a). However, the masses of oocytes and egg capsules were not significantly different.

Non-pregnant adult females were subdivided into three categories of specimens: post-partum, with vitellogenic activity and in complete break phase (Tab. II). Post-partum females exhibited a conspicuous vitellogenic activity and distended uteri showed placental attachment sites. By contrast, the second category of adult females comprised non-virgin specimens exhibiting active vitellogenesis with oocytes between 15 and 21-23 mm in diameter, the largest ones were yolky oocytes ready to be ovulated. The third category comprised non-virgin adult females with developed genital duct; however, the ovary showed no sign of vitellogenic activity and the uteri were empty, without placental attachment sites, they were considered in complete resting phase. They were generally large specimens between 112 and 150 cm TL and weighing between 4.5 and 8.1 kg.

In table III, we have included all females carrying developing embryos. Concerning near-term females and females carrying encapsulated eggs, we have only included for these two categories of adult females the largest specimens observed monthly.

Table II reveals that most females carrying encapsulated eggs, post-partum females and near-term females occurred between April and July; this suggests that gestation period was between 9-15 months, probably one year was the most appropriate duration. Records 14, 21 to 24, 25, 26, 2 to 4, 7, 8, 10 to 13, 15, 16, 17 showed a regular increase in size and mass in embryos, and confirmed a gestation period not exceeding one year approximately, as a suitable hypothesis.

Seventy-seven developing embryos were counted in left uterus *versus* 85 in right uterus (Tab. III), the counts were practically the same for term embryos (Tab. IV).

Forty-two embryos were observed, ranging in size between 100 and 126 mm TL (mean: 115 ± 6.8) and weighing between 8.4 and 13.6 g; they were recorded in four females, three caught in August (Tab. III, records 21, 22 and 23) and one in September (Tab. III, record 24). Both uteri were folded especially at their distal end but not yet compartmented, the embryos were non-pigmented, free in uteri. The umbilical cord was unadorned and smooth, and it was between 115 and 130 mm total length (mean: 121.4 ± 3.9). The yolk sac was slightly vascularized and contained a large quantity of yolk; it weighed (yolk included) between 6.5 and 7.9 g (mean: 7.3 ± 0.6). The embryos did not adhere to uterine wall and were partially dependent on their yolk reserves. External gill filaments were well developed. The embryos could be sexed and females (22) slightly outnumbered males (20). Embryos between 170 and 192 mm TL (mean: 179.2 ± 5.5) and weighing between 23 and 29 g (mean: 27.7 ± 1.8) were pigmented, and the length of external gill filaments were considerably reduced. They were in chamber and the umbilical stalk started to adhere to the uterine wall; its length was between 160 and 166 mm (mean: 162.2 ± 2.2) and the yolk sac contained a lot of yolk and weighed between 6.6 and 7.8 g (mean: 7.2 ± 0.4). They were still in a lecithotrophic phase. The 18 embryos equally distributed in each uterus, nine were males and nine females. Embryos were completely formed when they reached between 200 and 225 mm TL (mean: 206.8 ± 8.4) and weighed between 40 and 46 g (mean: 42.8 ± 1.7); the spiracle was visible and the external gill filaments were practically resorbed. Embryos strongly adhered to the uterine wall by an umbilical cord and the yolk was practically reabsorbed by the embryos, which are nourished by mother's uterine fluid. They were in a matrotrophic phase (Tab. III, records 2, 3 and 4). The umbilical cord was between 172 and 193 mm TL (mean: 180.7 ± 7.3) and the yolk sac weighed between 6.5 and 7.8 g (mean: 7.3 ± 0.6). The spiracle was obviously visible in embryos between 279 and 340 mm TL (mean: 308.7 ± 13.3) and weighing between 60 and 89 g (mean: 73.4 ± 8.3), (Tab. III, records 7, 8 and 10), no external gill filaments were visible, the umbilical cord lengthened, at about 300-340 mm TL (mean: 317.6 ± 14.4) and the yolk sac mass did not show changes although the yolk had completely disappeared (6.7-7.2 g, mean: 6.7 ± 0.3). In further embryonic stages, no important changes occurred, embryos slightly increased in length, by contrast they grew considerably in mass. So, term embryos were more robust and heavier than previous stages (Tab. III, IV). Yolk sac strongly adhered to uterine wall, which was obviously vascularized, convoluted and folded at the implantation site. Length of the umbilical cord measured in 221 term embryos was from 300 to 420 mm (mean: 337.7 ± 21.5); the mass of these term embryos was between 4.7 and 8.7 g (mean: 5.5 ± 0.5).

Size and mass

Measurements carried out on 221 term-embryos (Tab. IV), showed that TL ranged between 360 and 450 mm (mean: 403.1 ± 17.2) and mass between 155 and 256 g (mean: 199.9 ± 20.7). The five smallest free-swimming specimens, three males and two females, we have observed were between 390 and 420 mm TL (mean: 398.6 ± 12.4) and weighed between 195 and 202 g (mean: 206.2 ± 16.3). They bore an unhealed scar on the ventral surface and were probably neonates. No significant differences occurred in size and mass between them and term embryos.

The relationship between total mass (TM) and total length (TL), plotted in figure 3, shows no significant differences between males and females (F = 2.89; p = 0.09);

For males: log TM = 3.17 log TL - 5.97; n = 97; r = 0.97

For females: log TM = 3.37 log TL - 6.59; n = 174; r = 0.96

Fresh masses of forty-two yolky oocytes were from 3.6 to 4.9 g (mean: 4.2 ± 0.8), and 211 term embryos were from 155 to 256 g (mean: 119.9 ± 20.7). CBD based on mean dry masses for *M. mustelus* was 24.

Fecundity

Ovarian fecundity was based on counts of the number of yolky oocytes ready to be ovulated in each near-term female and post-partum female. Ovarian fecundity ranged from four to 25 (mean: 11.5 ± 3.6). There is a slight positive relationship between number of oocytes and total length of females, as: oocyte number = 0.08 TL (mm) - 10.92; r = 0.6; n = 65.

Uterine fecundity was based on content of both uteri comprising the number of encapsulated eggs or developing embryos or term embryos found in mother's uteri. It ranged from four to 24 (mean: 9.9 ± 4.3). There was also a slight positive relationship between uterine content and total length of females, as: uterine content = 0.025 TL (mm) - 20.53; r = 0.6; n = 80.

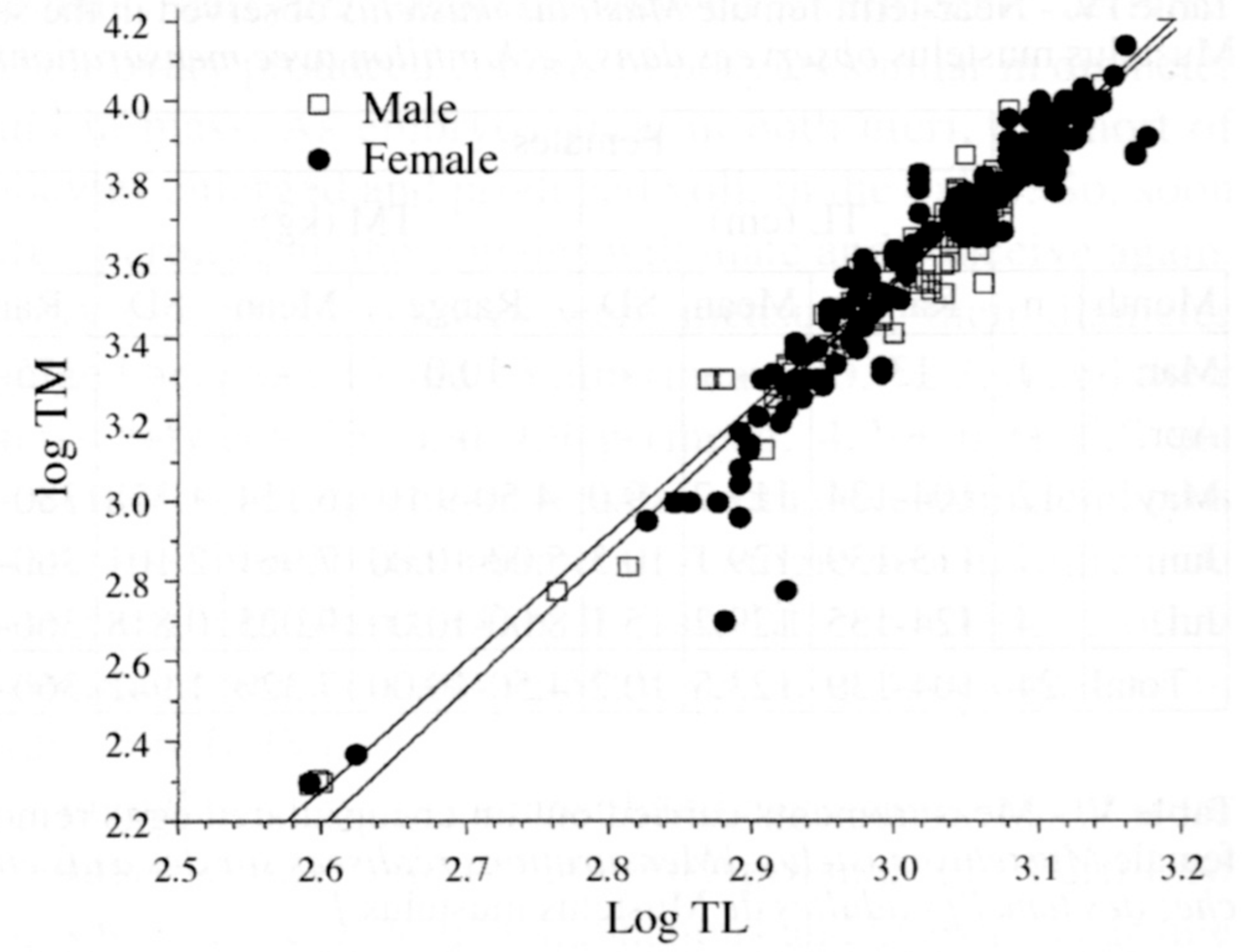

Figure 3. - Total mass (TM) *versus* total length (TL) expressed in logarithmic co-ordinates for male and for female *Mustelus mustelus*. *[Relation entre la masse totale (TM) et la longueur totale (TL) exprimée en coordonnées logarithmiques pour les mâles et les femelles de* Mustelus mustelus.*]*

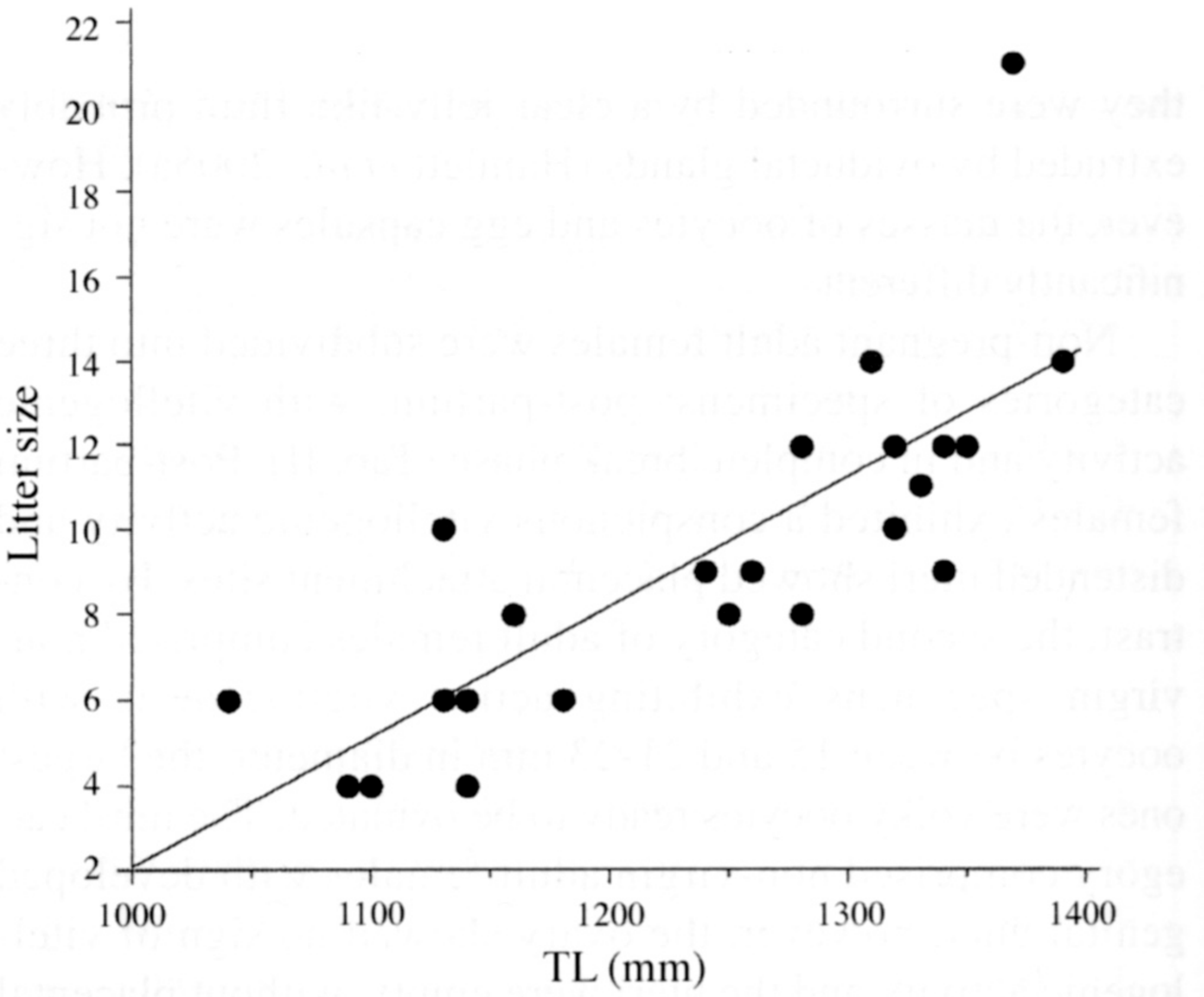

Figure 4. - Litter size versus total length (TL, mm) in *Mustelus mustelus*. *[Taille des portées en fonction de la longueur totale (TL, mm) chez* Mustelus mustelus.*]*

Litter size was based on the number of term embryos counted in females at the end of gestation. It ranged from four to 21 (mean: 9.2 ± 3.9). It increased with total length of females (Fig. 4), as: litter size = 0.03 TL (mm) - 28.28; r = 0.8; n = 24.

Sex-ratio

Females slightly outnumbered males in both categories of embryos, but these differences were not significant. However, in the three categories of free-swimming specimens we have considered, only sub-adult females significantly outnumbered the male ones (Tab. VI).

Table VI. - *Mustelus mustelus* sex-ratio for each category of specimens and for the total sample. *[Sex-ratio chez* Mustelus mustelus *pour chaque catégorie de spécimens et pour l'ensemble de l'échantillon.]*

Category	Males	Females	Males: Females
Uterine content			
Developing embryos	75	77	1: 1.03
Term embryos	102	119	1: 1.17
Total uterine content	177	196	1: 1.11
Free-swimming specimens			
Juveniles	6	15	1: 2.5
Sub-adults	12	44	1: 3.6
Adults	79	116	1: 1.5
Total free-swimming specimens	97	175	1: 1.8
Grand total	274	381	1: 1.4

DISCUSSION

The smoothhound, *Mustelus mustelus*, is only known in the Mediterranean and the eastern Atlantic (Branstetter, 1984; Compagno, 1984) and the southeastern coast of Africa (Bass *et al.*, 1975; Smale and Compagno, 1997) where populations are commercially exploited. However, in some Mediterranean areas such as the coast of Languedoc, a constant decline of captures was reported by Capapé *et al.* (2000) and the species has practically disappeared. By contrast, off Tunisia, *M. mustelus* is commonly landed (Capapé, 1974, 1989) and southward, it is targeted in the Gulf of Gabès (Bradaï *et al.*, 2002, 2004). *M. mustelus* was the focus of an intensive fishery in the eastern tropical Atlantic (Fischer *et al.*, 1981), and off Senegal, the species was always considered as common (Cadenat, 1951; Cadenat and Blache, 1981; Séret and Opic, 1990; Capapé *et al.*, 1994), a sustainable population seemed to be definitively established in the area, as shown by females carrying encapsulated eggs, or developing embryos or term embryos (Tab. I, II) and by records of specimens of both sexes and varied sizes.

Off the coast of Senegal, male *M. mustelus* matured at a smaller size than females did and reached smaller maximal size, which confirmed preliminary observations (Cadenat and Blache, 1981; Capapé *et al.*, 1994). Similar patterns were observed by Capapé (1974) for specimens from the Tunisian coast and by Smale and Compagno (1997) for those from off South Africa. However, although *M. mustelus* from the two latter areas matured at a larger size than the Senegalese ones, specimens of all areas did not show important differences in maximal size (Tab. VII). This suggests that different populations occurred in each area. Difference in size related to environmental parameters was described for oviparous species (Leloup and Olivereau, 1951), but this hypothesis needs further observation with special regard to viviparous species (Dodd, 1983; Capapé *et al.*, 2001).

By contrast, table VII showed that sizes at birth are in agreement in the three areas. Ranzi (1932) noted that in the Bay of Naples, term embryo was 380 mm TL and weighed 189.6 g. However, off British Isles, Wheeler (1969) noted 300 mm only for term embryos. In all areas, as noted by Smale and Compagno (1997): "There was a notable variation in the size of individuals within a litter". They explained this phenomenon by duration of ovulation, and the vascularization that is different in the different parts of uteri. Similar patterns were observed in other placental viviparous species such as carcharhinids (Capapé *et al.*, 2003, 2004).

Ranges of litter sizes are also similar in the three areas (Tab. VII). Off Naples, southern Italy, Lo Bianco (1909) recorded 28 embryos in a pregnant female.

Lo Bianco (1909) and Smale and Compagno (1997) reported similar stages in embryonic development to those described in the present article (see above). Smale and Compagno (1997) noted that embryos less than 121-145 mm total length were still free in the uteri. They added that over 200-252 mm TL, the placenta strongly adhered to the uterine wall, which was highly vascularized.

Off the coast of Senegal, mating probably occurred from April to June, when both male and female adults were most encountered in the area (Tab. I). The relative abundance of

Table VII. - Comparisons of size at sexual maturity, maximal size, size at birth and litter size in *Mustelus mustelus* from Mediterranean, South Africa and coast of Senegal. *[Comparaisons entre les tailles de maturité sexuelle, taille maximale, taille à la naissance et taille des portées chez* Mustelus mustelus *de Méditerranée, Afrique du Sud et côte du Sénégal.]*

Area	Size at sexual maturity (TL, cm)		Maximal size (TL, cm)		Size at birth (TL, cm)	Litter size	Authors
	Males	Females	Males	Females			
Gulf of Tunis (Northern Tunisia)	960	108-117	-	142	39.0	12-22	Capapé, 1974
South Africa	95-105	125-140	145	165	36.8-41.0	2-23	Smale and Compagno (1997)
Coast of Languedoc (Southern France)	> 98	> 98	123	123	38.0-42.0	-	Capapé *et al.* (2000)
Coast of Senegal	82-89	90-104	139	145	36.0-45.0	4-21	This study

post-partum females and females carrying term embryos showed that parturition occurred between April and July. The captures of females carrying encapsulated eggs, post-partum females and near-term females suggest that a one year gestation period seems to be a suitable hypothesis for specimens from off the coast of Senegal, in agreement with Capapé observations (1974) for specimens from the Gulf of Tunis. However, in this area, mating occurred in May and parturition in April-May. Off South Africa, Smale and Compagno (1997) noted that the gestation period was about 9-11 months. Lo Bianco (1909) reported a gestation period of ten months for *M. mustelus* from off Naples.

We found that off Senegal, as embryos of *M. mustelus* developed in the uteri, the ovary showed conspicuous vitellogenic activity, a crop of yolky oocytes is ovulated soon after parturition, beginning a new reproductive cycle. *Mustelus mustelus* therefore reproduced annually in the Senegalese waters, as was the case for specimens from the Gulf of Tunis (Capapé, 1974), South Africa (Smale and Compagno, 1997). This holds for other congeneric species such as *M. griseus* and *M. manazo* from Japan (Teshima *et al.*, 1974), *M. punctulatus* and *M. asterias* from the Gulf of Tunis (Capapé and Quignard, 1977; Capapé, 1983), and *M. antarcticus* and *M. canis* (Hamlett *et al.*, 1993). However, we observed adult females in complete break phase in our sample (see Tab. II), as was noted in 40 % of quarterly samples in *M. mustelus* from South Africa (Smale and Compagno, 1997). Consequently, some females could reproduce in alternate years, or every three years. Similar patterns were also found in *Rhizoprionodon acutus* (Capapé, unpubl. data), in *Paragaleus pectoralis* from the coast of Senegal (Capapé *et al.*, 2005) and in some carcharhinid species (Capapé, 1984; Capapé *et al.*, 2003, 2004; Saïdi *et al.*, 2005).

Embryonic development in *M. mustelus* is very similar to that previously described in other placental viviparous species such as triakid species (Capapé and Quignard, 1977; Smale and Compagno, 1997; Capapé *et al.*, 2000), or carcharhinid species (Baranes and Wendling, 1981; Castro and Wourms, 1993; Hamlett *et al.*, 1993; Capapé *et al.*, 2003, 2004). Embryonic development comprised three stages. During the first stage, the embryos were free in uteri, rather lecithotrophic because nourished by the yolk stored in the yolk sac; gas exchange probably occurred through the yolk sac and the intertegument (Castro and Wourms, 1993; Smale and Compagno, 1997). This phase could last less than three months maximum. The second stage was intermediate between lecithotrophy and matrotrophy. It ended when embryos adhered to uterine wall and reached more than 121-145 mm TL (see above) and lasted less than two months. The third stage lasted at least six months and was exclusively matrotrophic; gas exchange occurred probably through the placenta (Castro and Wourms, 1993; Hamlett *et al.*, 1993). Similar observations were reported by Teshima and Koga (1973) in Japanese *M. griseus*, and by Smale and Compagno (1997) in South African *M. mustelus*. The high CBD value, 24, is close to those previously calculated for the two sympatric species, *P. galeus* and *R. acutus*, inhabiting Senegalese waters, which were 15 and 23, respectively. These data showed the mother's role in these placental viviparous elasmobranch species, which are pure matrotrophic species (*sensu* Wourms, 1977, 1981; Wourms *et al.*, 1988; Hamlett *et al.*, 2005b). Similar values were previously reported in other sharks, (Capapé *et al.*, 2003, 2004) and rays (Capapé *et al.*, 1992, Capapé, 1993, Capapé and Zaouali, 1995).

Both ovarian and uterine fecundities are slightly related to total length of females. Similar patterns were observed for *M. mustelus* from the Gulf of Tunis (Capapé, 1974). Smale and Compagno (1997) noted that "there was a significant trend for larger females to have larger litters". Litter sizes of specimens from the Mediterranean Sea (Lo Bianco, 1909; Capapé, 1974), South Africa (Smale and Compagno, 1997) and Senegal (this study) are very similar. However, in agreement with Smale and Compagno (1997), "there may be a maximum litter size". Twenty-eight was the highest value reported to date (Lo Bianco, 1909), consequently, in agreement with Tortonese (1956), we think that 60 neonates reported in a litter by Duméril (1865) remains doubtful. Ovarian fecundity is slightly higher than uterine fecundity; this phenomenon was frequently observed in viviparous elasmobranch species, due to fact that some yolky oocytes were not ovulated and entered atresia, and unfertilized eggs did not develop in uteri (Smale and Compagno, 1997). This latter phenomenon was observed relatively more often in *M. mustelus* than in other placental viviparous elasmobranchs. Although abortion risks cannot be excluded, especially during captures and handling, developing embryos in *M. mustelus* were well-protected in chambers and strongly adherent to uterine wall by placenta.

In uteri, both developing and term embryos males slightly outnumbered the female ones, in agreement with Stevens and McLoughlin (1991) who also noted that generally embryos are distributed in equal numbers in each uteri (Waller and Baranes, 1994; Smale and Goosen, 1999; Capapé *et al.*, 2003, 2004). In three categories of free-swimming specimens, only sub-adult females significantly outnumbered the male ones. Olsen (1954) and Springer (1960) suggested a higher mortality rate in males for *Galeorhinus galeus* and *C. plumbeus*, respectively. Muñoz-Chapuli (1984) and Stevens and McLoughlin (1991) suggested a segregation by size in free-swimming specimens and sexual segregation in adults. The coast of Senegal was considered by Capapé *et al.* (1998, 2003, 2004, 2005) as a probable nursery area for several shark species (Castro, 1993), including the smouthhound which is commonly captured in the area, although a competition pressure cannot be excluded, with species of larger sizes (Cadenat, 1951; Cadenat and Blache, 1981; Séret and Opic, 1990; Capapé *et al.*, 1994, 1998, 2003, 2004).

Acknowledgements. - The authors thank two anonymous referees for helpful and useful comments on the ms. They are also grateful to Bernard Séret from MNHN, Paris for sending important papers and encouragements.

REFERENCES

BARANES A. & J. WENDLING, 1981. - The early stages of development in *Carcharhinus plumbeus*. *J. Fish Biol.*, 18: 159-175.

BASS A.J., D'AUBREY J.D. & N. KISTNASAMY, 1975. - Sharks of the East coast of Southern Africa. III. The families Carcharhinidae (excluding *Mustelus* and *Carcharhinus*) and Sphyrnidae. *Invest. Rep. Ocean. Res. Inst.*, 33: 1-100.

BRADAÏ M.N., SAÏDI B., GHORBEL M., BOUAÏN A., GUÉLORGET O. & C. CAPAPÉ, 2002. - Observations sur les requins du golfe de Gabès (Tunisie méridionale, Méditerranée centrale). *Mésogée*, 60: 61-77.

BRADAÏ M.N., QUIGNARD J. P., BOUAÏN A., JARBOUI O., OUANNES-GHORBEL A., BEN ABDALLAH L., ZAOUALI J. & S. BEN SALEM. 2004. - Ichtyofaune autochtone et exotique des côtes tunisiennes: recensement et biogéographie. *Cybium*, 28(4): 315-328.

BRANSTETTER S., 1984. - Triakidae. *In*: Fishes of the North-Eastern Atlantic and Mediterranean/ Poissons de l'Atlantique du Nord-Est et de la Méditerranée, Vol. 1 (Whitehead P.J.P., Tortonese E., Bauchot M.-L., Hureau J.-C. & J. Nielsen, eds), pp. 117-121. Paris: UNESCO.

BRIDGE N.F., McKAY D. & G. NEWTON, 1998. - Biology of the ornate angel shark (*Squatina tergocellata*) from the Great Australian Bight. *Mar. Freshw. Res.*, 49: 679-686.

CADENAT J., 1951. - Poissons de mer du Sénégal. *Init. Afr., Inst. Fr. Afr. Noire, Dakar*, 3: 1-345.

CADENAT J. & J. BLACHE, 1981. - Requins de Méditerranée et d'Atlantique (plus particulièrement de la côte occidentale d'Afrique). *Faune Trop.*, ORSTOM, 21: 1-330.

CALLARD I.P., GEORGE J.S. & T.J. KOOB, 2005. - Endocrine control of the female reproductive tract. *In*: Reproductive Biology and Phylogeny of Chondrichthyes. Sharks, Batoids and Chimaeras (Hamlett W.C., ed.), pp. 283-300. Enfield (NH, USA), Plymouth (UK): Sciences Publishers, Inc.

CAPAPÉ C., 1974. - Observations sur la sexualité, la reproduction et la fécondité de 8 Sélaciens pleurotrêmes vivipares placentaires des côtes tunisiennes. *Arch. Inst. Pasteur, Tunis*, 51: 329-344.

CAPAPÉ C., 1983. - Nouvelles données sur la biologie de la reproduction de *Mustelus asterias* Cloquet, 1821 (Pisces, Pleurotremata, Triakidæ) des côtes tunisiennes. *Vie Milieu*, 33(3-4): 143-152.

CAPAPÉ C., 1984. - Nouvelles données sur la morphologie et la biologie de la reproduction de *Carcharhinus plumbeus* (Nardo, 1827) (Pisces, Carcharhinidæ) des côtes tunisiennes. *Inv. Pesq.*, 48(2): 115-137.

CAPAPÉ C., 1989. - Les Sélaciens des côtes méditerranéennes : aspects généraux de leur écologie et exemples de peuplements. *Océanis*, 15(3): 309-331.

CAPAPÉ C., 1993. - New data on the reproductive biology of the thorny stingray, *Dasyatis centroura* (Mitchill, 1815), from off the Tunisian coasts. *Env. Biol. Fish.*, 38: 73-80.

CAPAPÉ C. & J.P. QUIGNARD, 1977. - Contribution à la biologie des Triakidæ des côtes tunisiennes. I. *Mustelus mediterraneus* Quignard et Capapé, 1972 : répartition géographique et bathymétrique, migrations et déplacements, reproduction, fécondité. *Bull. Off. Natl. Pêch. Tunisie*, 1(2): 169-172.

CAPAPÉ C. & J. ZAOUALI, 1995. - Reproductive biology of the marbled stingray, *Dasyatis marmorata* (Steindachner, 1892) (Pisces: Dasyatidæ) in the Tunisian waters. *J. Aquaricult. Aquat. Sci.*, 7: 108-119.

CAPAPÉ C., QUIGNARD J.P. & J. MELLINGER, 1990. - Reproduction and development of two angel sharks, *Squatina squatina* and *S. oculata* (Pisces: Squatinidae), off Tunisian coasts: semi-delayed vitellogenesis, lack of egg capsule and lecithotrophy. *J. Fish Biol.*, 37: 347-356.

CAPAPÉ C., ZAOUALI J., TOMASINI J.P. & J.L. BOUCHEREAU, 1992. - Reproductive biology of the spiny butterfly ray, *Gymnura altavela* (Linnaeus, 1758) (Pisces: Gymnuridae) from off the Tunisian coasts. *Sci. Mar.*, 56: 347-55.

CAPAPÉ C., DIOP M. & M. N'DAO, 1994. - Observations sur la biologie de la reproduction de dix-sept espèces de Sélaciens d'intérêt économique capturés dans la région marine de Dakar-Ouakam (Sénégal, Atlantique oriental tropical). *Bull. Inst. Fond. Afr. Noire Cheikh Anta Diop, Dakar*, sér. A, 47: 87-102.

CAPAPÉ C., DIOP M., & M. N'DAO, 1998. - Record of four pregnant females of the scalloped hammerhead, *Sphyrna lewini* (Sphyrnidae) in Senegalese waters (Eastern Tropical Atlantic). *Cybium*, 22(1): 89-93.

CAPAPÉ C., TOMASINI J.A. &. J.P. QUIGNARD, 2000. - Les Élasmobranches Pleurotrêmes de la côte du Languedoc (France méridionale, Méditerranée septentrionale). Observations biologiques et démographiques. *Vie Milieu*, 50(2): 123-133.

CAPAPÉ C., BRADAÏ M.N., SECK A.A., DIATTA Y., TOMASINI J.A., QUIGNARD J.P. 2001. - Aspects of the reproductive biology of the Velvet Belly, *Etmopterus spinax* (Elasmobranchii: Squalidae). *Bull. Inst. Sci. Techn. Mer Salammbô*, 28: 55-64.

CAPAPÉ C., SECK A.A., GUEYE-NDIAYE A., DIATTA Y., & M. DIOP, 2002. - Reproductive biology of the smooth angelshark, *Squatina oculata* (Elasmobranchii: Squatinidae), from the coast of Senegal (eastern tropical Atlantic). *J. Mar. Biol. Ass. UK*, 82: 635-640.

CAPAPÉ C., HEMIDA F., SECK A.A., DIATTA Y., GUÉLORGET O. & J. ZAOUALI, 2003. - Distribution and reproductive biology of the spinner shark, *Carcharhinus brevipinna* (Müller and Henle, 1841) (Chondrichthyes: Carcharhinidae). *Isr. J. Zool.*, 49(3): 269-286.

CAPAPÉ C., SECK A.A., DIATTA Y., REYNAUD C., HEMIDA F. & J. ZAOUALI, 2004. - Reproductive biology of the blacktip shark, *Carcharhinus limbatus* (Chondrichthyes: Carcharhinidae) off west and north African coasts. *Cybium*, 28(4): 275-284.

CAPAPÉ C., DIATTA Y., DIOP M., REYNAUD C. & O. GUÉLORGET, 2005. - New data on the reproductive biology of the Atlantic weasel shark, *Paragaleus pectoralis* (Chondrichthyes: Hemigaleidae) from the coast of Senegal (Eastern Tropical Atlantic). *Cybium*, 29(4): 363-371.

CASTRO J.L., 1993. - The shark nursery of Bulls Bay, South Carolina, with a review of the sharks nurseries of the southeastern coast of the United States. *Env. Biol. Fish.*, 38: 37-48.

CASTRO J.I & J.P. WOURMS, 1993. - Reproduction, placentation and embryonic development of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. *J. Morphol.*, 218: 257-280.

COLLENOT G., 1969. - Étude biométrique de la croissance relative des ptérygopodes chez la roussette *Scyliorhinus canicula* L. *Cah. Biol. Mar.*, 10: 309-29.

COMPAGNO L.J.V., 1984. - FAO species catalogue. Vol 4. Sharks of the world. An annotated and illustrated catalogue of sharks species known to date. Part 2. Carcharhiniformes. *FAO Fish. Syn.*, 125: 251-655.

DODD J.M., 1983. - Reproduction. *In*: Fish Physiology, Vol. 1 (Hoar W.S., Randall D.J. & E.M. Donaldson, eds), pp. 31-95. New-York: Academic Press.

DUMÉRIL A.H.A., 1865. - Histoire générale des poissons ou ichtyologie générale. 720 p. Paris.

FISCHER W., BIANCHI G. & W.B. SCOTT, 1981. - Fiches FAO d'identification des espèces pour les besoins de la pêche. Atlantique centre-est ; zones de pêche 34, 47 (en partie). Canada Fond de Dépôt. Ottawa, Ministère des Pêcheries et Océans du Canada, en accord avec l'organisation des Nations-Unies pour l'Alimentation et l'Agriculture, Vol. 165, pag. var.

GUEYE-NDIAYE A., 1993. - La transformation artisanale des produits halieutiques sur le littoral et son impact sur l'environnement. *In*: Gestion des Ressources côtières et littorales du Sénégal. Actes de l'Atelier de Gorée (Sénégal), juillet 1992 (Diaw A.T., Bâ A., Bouland P., Diouf P.S., Lake L.-A., Mbow M.-A., Ndiaye P. & M.D. Thiam, eds), pp. 323-334. Gland (Suisse): UICN.

HAMLETT W.C., EULITT A.M., JARELL J.R. & M.A. KELLY, 1993. - Uterogestation and placentation in elasmobranchs. *J. Exp. Zool.*, 266: 347-367.

HAMLETT W.C., HYSELL M.K., ROZYCKI T., BRUNETTE N., TUMILTY K., HENDERSON. A. & J. DUNNE, 1999. - Sperm aggregation and spermatozeugma formation in the male genital ducts in the clearnose skate, *Raja eglanteria*. *In*: Proc. 5th Indo-Pac. Fish Conf. Nouméa, Nov. 1997 (Séret B. & J.Y. Sire, eds), pp. 281-291. Paris: Soc. Fr. Ichthyol. & ORSTOM.

HAMLETT W.C., KNIGHT D.P., PEREIRA F.T.V., STEELE J. & D.M. SEVER, 2005a. - Oviducal glands in Chondrichthyans. *In*: Reproductive Biology and Phylogeny of Chondrichthyes. Sharks, Batoids and Chimaeras (Hamlett W.C., ed.), pp. 301-335. Enfield (NH, USA), Plymouth (UK): Sciences Publishers, Inc.

HAMLETT W.C., KORMANIK G., STORRIE M., STEVENS B. & T.I. STEVENS, 2005b. - Chondrichthyan parity, lecithotrophy and matrotrophy. *In*: Reproductive Biology and Phylogeny of Chondrichthyes. Sharks, Batoids and Chimaeras (Hamlett W.C., ed.), pp. 395-434. Enfield (NH, USA), Plymouth (UK): Sciences Publishers, Inc.

KÉBÉ M. & L. LE RESTE, 1993. - Conflits liés au secteur des pêches sénégalaises. *In*: Gestion des ressources côtières et littorales du Sénégal. Actes de l'Atelier de Gorée (Sénégal), juillet 1992 (Diaw A.T., Bâ A., Bouland P., Diouf P.S., Lake L.-A., Mbow M.-A., Ndiaye P. & M.D. Thiam, eds), pp. 379-392. Gland (Suisse): UICN.

LELOUP J. & M. OLIVEREAU, 1951. - Données biométriques comparatives sur la Roussette (*Scyllium canicula* L.) de la Manche et de la Méditerranée. *Vie Milieu*, 2: 182-206.

LO BIANCO S., 1909. - Notizie biologiche riguardanti specialmente il periodo di maturità sessuale degli animali del golfo di Napoli. *Mitt. Zool. Stn, Neapel*, 19(4): 513-761.

MELLINGER J. & J. WRISEZ, 1989. - Biologie et physiologie comparée de deux sélaciens ovipares, les roussettes *Scyliorhinus canicula* et *Scyliorhinus stellaris*. Evolution de la matière sèche, de l'eau et des ions (Cl^-, Na^+, K^+) dans le vitellus de *S. canicula* au cours du développement. *Bull. Soc. Zool. Fr.*, 114: 51-62.

MUÑOZ-CHAPULI R., 1984. - Éthologie de la reproduction chez quelques requins de l'Atlantique-Nord. *Cybium*, 8(1): 1-14.

OLSEN A.M., 1954. - The biology, migration and growth rate of the school shark, *Galeorhinus australis* (Macleay) (Carcharhinidae) in southeastern Australian waters. *Aust. J. Mar. Freshw. Res.*, 5: 353-410.

RANZI S., 1932. - Le basi fisio-morfologiche dello sviluppo embrionale dei selaci. *I. Pubb. Sta. Zool. Napoli*, 12: 209-290.

SAÏDI B., BRADAÏ M.N., BOUAÏN A., GUÉLORGET O. & C. CAPAPÉ, 2005. - New data on the reproductive biology of the sandbar shark, *Carcharhinus plumbeus* (Chondrichthyes: Carcharhinidae) from the Gulf of Gabès (Southern Tunisia, Central Mediterranean). *Acta. Adriat.*, 46(1): 47-62.

SÉRET B. & P. OPIC, 1990. - Poissons de mer de l'ouest africain tropical. Init.-Doc., 49. Paris: ORSTOM, 416 p.

SMALE M.J. & L.V.J. COMPAGNO, 1997. - Life history and diet of two southern African smoothhound sharks, *Mustelus mustelus* (Linnaeus, 1758) and *Mustelus palumbes* Smith, 1957 (Pisces: Triakidae). *S. Afr. Mar. Sci.*, 18: 229-248.

SMALE M.J. & A.J.J. GOOSEN, 1999. - Reproduction and feeding of spotted gully shark, *Triakis megalopterus*, off the Eastern Cape, South Africa. *Fish. Bull.*, 97: 987-998.

SPRINGER S., 1960. - Natural history of the sandbar shark *Eulamia milberti*. *Fish. Bull. Fish Wildl. Ser. U.S.*, 178: 1-38.

STEVENS J.D. & K.J. McLOUGHLIN, 1991. - Distribution, size and sex composition, reproductive biology and diet of sharks from Northern Australia. *Aust. J. Mar. Freshw. Res.*, 42: 151-99.

TESHIMA K. & S. KOGA, 1973. - Studies on sharks. V. Taxonomic characteristics of reproductive organs in Japanese *Mustelus*. *Mar. Biol.*, 23: 337-341.

TESHIMA K., MIZUE K. & S. KOGA, 1974. - Studies on sharks. VII. Reproduction in female *Mustelus griseus*. *J. Shimonoseki Univ. Fish.*, 22(3): 85-92.

TORTONESE E., 1956. - Leptocardia, Ciclostomata, Selachii. *In*: Fauna d'Italia, 2. 332 p. Bologna: Calderini.

WALLER G.N.H. & A. BARANES, 1994. - Food of *Iago omanensis*, a deep water shark from the northern Red Sea. *J. Fish Biol.*, 45: 37-45.

WATSON G. & M.J. SMALE, 1998. - Reproductive biology of shortnose spiny dogfish, *Squalus megalops*, from the Agulhas Bank, South Africa. *Mar. Freshw. Res.*, 49: 695-703.

WHEELER A., 1969. - The Fishes of the British Isles and North-West Europe. 163 p. London, Melbourne and Toronto: Mc Millan.

WOURMS J.P., 1977. - Reproduction and gestation in Chondrichthyans fishes. *Am. Zool.*, 17: 379-410.

WOURMS J.P., 1981. - Viviparity: The maternal-fetal relationship in fishes. *Am. Zool.*, 21: 473-515.

WOURMS J.P., GROOVE J.P. & J. LOMBARDI, 1988. - The maternal-embryonic relationship in viviparous fishes. *In*: Fish Physiology, Vol. 1 (Hoar W.S., Randall D.J. & E.M. Donaldson, eds), pp. 1-134. New-York: Academic Press.

Reçu le 10 mai 2005.
Accepté pour publication le 10 mars 2006.